Title: Individuals in urban dwelling primate species face unequal benefits associated with living in an anthropogenic environment

Authors: Pascal R. Marty[1,2]*, Krishna N. Balasubramaniam[1], Stefano S. K. Kaburu[1,3], Josephine Hubbard[1], Brianne Beisner[1,4], Eliza Bliss-Moreau[4,5], Nadine Ruppert[2], Małgorzata E. Arlet[6], Shahrul Anuar Mohd Sah[2], Ahmad Ismail[7], Lalit Mohan[8], Sandeep K. Rattan[8], Ullasa Kodandaramaiah[9], Brenda McCowan[1,4]

Affiliations: [1]Department of Population Health & Reproduction, School of Veterinary Medicine, University of California, Davis, USA

[2]School of Biological Sciences, Universiti Sains Malaysia, 11800 Pulau Pinang, Malaysia

[3]Department of Biomedical Science & Physiology, Faculty of Science & Engineering, University of Wolverhampton, Wolverhampton, WV1 1LY, UK

[4]California National Primate Research Center, University of California, Davis, USA

[5]Department of Psychology, University of California, Davis, USA

[6]Adam Mickiewicz University, Anthropology Institute, Poznań 61614, Poland

[7]Department of Biology, Faculty of Science, Universiti Putra Malaysia, 43400 UPM Selangor, Malaysia

[8]Himachal Pradesh Forest Department, Shimla, Himachal Pradesh, 171002, India

[9]IISER-TVM Centre for Research and Education in Ecology and Evolution (ICREEE), School of Biology, Indian Institute of Science Education and Research Thiruvananthapuram, Maruthamala P.O., Vithura, Thiruvananthapuram, India. 695551

Corresponding author:

Pascal R. Marty, Department of Population Health and Reproduction, School of Veterinary Medicine, University of California, 1089 Veterinary Medicine Dr., Davis, CA 95616 (US), E-Mail: pmarty@ucdavis.edu, Phone: +1 (530) 220 07 38

Abstract:

In primates, living in an anthropogenic environment can significantly improve an individual's fitness, which is likely to be attributed to access to anthropogenic food resources. However, in non-professionally provisioned groups, few studies have examined whether individual attributes, such as dominance rank and sex, affect primates' ability to access anthropogenic food. Here, we investigated whether rank and sex explain individual differences in the proportion of anthropogenic food consumed by macaques. We observed 319 individuals living in nine urban groups across three macaque species. We used proportion of anthropogenic food in the diet as a proxy of access to those food resources. Males and high-ranking individuals in both sexes had significantly higher proportions of anthropogenic food in their diets than other individuals. We speculate that unequal access to anthropogenic food resources further increases within-group competition, and may limit fitness benefits in an anthropogenic environment to certain individuals.

Keywords: Anthropogenic food, Urban Environment, Macaques, Foraging

52

53 **Introduction**:

54 Animals living in anthropogenic environments face both costs and benefits associated
55 with such environments. While the costs are diverse, e.g. increased aggression both from
56 conspecifics (Southwick et al., 1976) and humans (McCarthy et al., 2009), chronic stress
57 (Marechal et al., 2011), culling or translocation (Berman et al., 2007; Malaivijitnond and
58 Hamada, 2008), the benefits are mainly limited to increased access to anthropogenic food
59 resources (hereafter called AFR) (Oro et al., 2013). Compared to natural food resources, AFR are
60 frequently higher in calories, and many (if not most) AFR have highly predictable locations and
61 timing of access. Such predictable foods may increase foraging efficiency, and ultimately
62 individual fitness of animals relying on AFR (Oro et al., 2013). A significant lower intake of
63 natural food in provisioned animals indicate that AFR are often preferred over natural food
64 resources (barbary macaques, *Macaca silvanus*: Maibeche et al., 2015; rhesus macaques,
65 *Macaca mulatta*: Sengupta and Radhakrishna, 2018; long-tailed macaques, *Macaca fascicularis*:
66 Sha and Hanya, 2013). Possibly from the benefits of foraging on AFR, non-human primate
67 (hereafter called primate) groups living in an anthropogenic environment experience decreased
68 interbirth intervals, lower infant mortality, as well as increased group sizes and population
69 densities (Altmann and Muruthi, 1988; Jaman and Huffman, 2013; Kurita et al., 2008; Warren et
70 al., 2011). Access to AFR is further associated with changes in activity budgets, diet, and social
71 interactions (Berman and Li, 2002; El Alami et al., 2012; Ilham et al., 2018; Kaburu et al., 2019;
72 Kaburu et al., 2019; Marty et al., 2019; McKinney, 2011). Any of these aspects may influence
73 animals' fitness (Marty et al., 2019). While the degree, consistency, amount and type of AFR

74 can vary greatly across populations and situations, a substantial number of primate groups do
75 have some access to such food resources, potentially affecting their behavior and fitness. Since
76 access to AFR may be directly linked to an individual's fitness, knowledge of those attributes
77 that influence inter-individual differences in access to AFR is crucial to understanding the
78 selection pressures on individuals living in an anthropogenic environment.

79 While more and more groups get access to some AFR, access is not equally distributed
80 across group members, but is likely dependent on the ability of some individuals to monopolize
81 these food resources. The monopolization potential of AFR is expected to follow a gradient
82 from professionally provisioned AFR that is confined to small spaces, to more widely distributed
83 AFR (e.g. Ram et al., 2003). Professionally provisioning occurs in situations where humans,
84 often from official positions in governmental, educational, or conservation organizations,
85 provision primates consistently and systematically, often to manage such populations for
86 tourism (e.g., Tibetan macaques, *Macaca thibetana*, of Mt. Huangshan, China: Berman et al.,
87 2007) or research purposes (e.g., rhesus macaques of Cayo Santiago: Hernandez-Pacheco et al.,
88 2016). The individual monopolization potential further decreases with an increased temporal
89 and spatial unpredictability of AFR. If the occurrence of AFR is less predictable in space and time
90 (e.g., food is provided throughout the day from several people at different locations),
91 individuals with a high monopolization potential will need time to get to the AFR before they
92 can prevent other individuals from accessing them.. In such situations, typically described as
93 opportunistic provisioning (e.g., food provisioning by visitors and local people), a lower
94 predictability and thus monopolization potential can be assumed (Ram et al. 2003). However,
95 compared to natural food, all AFR are generally considered to be more clumped and more

predictable in their spatial and temporal distribution (Becker and Hall, 2014; Koganezawa and Imaki, 1999; Saj et al., 1999; Strum, 1994; Warren et al., 2011). In summary, the distribution, size and predictability of AFR affect to what degree certain individuals can monopolize them.

Previous studies investigating access to AFR in primates have mainly focused on professionally provisioned groups. In general, these studies found a consistent pattern where the social position in a group predicted access to AFR. High-ranking female Japanese macaques (*Macaca fuscata*), Barbary macaques (*M. sylvanus*), and Yellow baboons (*Papio cynocephalus*), for example, were found to feed longer on AFR and stay longer at the feeding site than low-ranking females (Altmann and Muruthi, 1988; Fa, 1985; Kurita, 2007; Mori, 1995; Soumah and Yokota, 1991). In contrast, Ram et al. (2003) did not find rank-related access to AFR in opportunistically provisioned female bonnet macaques (*Macaca radiata*). The authors speculated that the spatial and temporal variation in provisioning decreased predictability of opportunistically provided food leads to a lower monopolization potential, thus rank would not predict access to such AFR. Finally, while patterns in access to AFR have been described in both professionally and opportunistically provisioned populations, most studies focused on female primates (Altmann and Muruthi, 1988; Mori, 1995; Soumah and Yokota, 1991), whereas males where either ignored or did not show a rank difference in time spent at the feeding site (Fa, 1985; Sapolsky and Share, 2004).

In this study, we aim to investigate access to AFR in opportunistically provisioned groups of three primate species (long-tailed macaques; *Macaca fascicularis*, rhesus macaques; *Macaca mulatta*, and bonnet macaques; *Macaca radiata*). None of the study groups were professionally provisioned, i.e. received food provided by the government or other organization(s). Instead,

they all had access to opportunistic food provisioning by visitors and local people. Despite being in between professionally provisioned and wild groups regarding the monopolization potential, we predict that access to AFR in opportunistically provisioned groups is biased towards males and high-ranking individuals since AFR are generally expected to be more predictable and clumped in comparison to natural food.

Methods:

We observed adult individuals in nine groups of primates ranging from temperate areas in Northern India, to tropical environments in Southern India and Malaysia (Table 1). In the northern Indian city of Shimla (31.05N, 77.1E), we observed four groups of rhesus macaques from June 2016 to February 2018 (for details on the study site see Kaburu et al. 2019a). From July 2017 until May 2018, we studied two groups of bonnet macaques in the Thenmala Dam and Ecotourism Recreational Area (8.90N, 77.10E) located at the outskirts of the small town of Thenmala within the state of Kerala in Southern India (Balasubramaniam et al. under review). In Malaysia, we observed four groups of long-tailed macaques in Kuala Lumpur, from September 2016 until February 2018 (for details on the study site see Marty et al., 2019). All groups were living in anthropogenic environments where visitors and tourists provided AFR to the monkeys. AFR in Malaysia mainly consisted of sweet and salty snacks (e.g., ice-cream/chips) and occasionally fruits. Apart from AFR, the long-tailed macaques in Malaysia mainly consumed leaves, flowers, seeds, and insects from the natural vegetation (personal observations) similar to forested groups (Yeager, 1996). The two sites differed considerably. While Batu Cave (groups MF3&4) (3.23N, 101.7E) is a tourist attraction with around 4000 visitors a day where the shared

interface is limited to flights of stairs and the temple, Templer Park (groups MF1&2)(3.29N, 101.6E) has around 150 visitors a day and contains multiple paths were people interacted with the monkeys (Marty et al. 2019). Among the rhesus macaques in Shimla, AFR was largely made up of sugar pellets called prasād, although occasionally macaques were fed with both sweet and salty snacks such as biscuits, chocolate and chips (Kaburu et al., 2019a; Kaburu et al., 2019b). In this site, macaques had also access to a forested area where they could feed on natural food sources, especially leaves and flowers (Kaburu et al., 2019a; Kaburu et al., 2019b). For the group MM1 the shared interface consisted of a road with the surrounding buildings whereas groups MM2,3&4 mainly interacted with people at the temple area (Kaburu et al., 2019a; Kaburu et al., 2019b). In Thenmala, bonnet macaques were provisioned, albeit less frequently compared to Shimla and Malaysia, with sweet or salty snacks (e.g., chips, ice-cream), spicy rice and wheat-based items (e.g., biryani, chapathis), and fruits (e.g., bananas). They also foraged on environmentally available foods, both anthropogenic (garbage, fruiting trees planted in gardens) and natural (insects, leaves and fruits from forest patches within their home-range). The shared interfaces for both groups (MR 1&2) consisted of roads, parking areas and garden areas (Balasubramaniam et al. under review). While the degree of provisioning from visitors differed between sites, none of the groups received any professionally provisioned food. Thus, the amount of AFR varied between days and locations within a groups home range.

Table 1: Demography of all study groups with number of males and females and the total observation time.

Species	Group	# of Males	# of Females	Observation time (h)

Macaca mulatta (Shimla, India)	MM1	6	17	275.3
	MM2	7	17	347.2
	MM3	12	43	487.2
	MM4	12	25	662.5
Macaca fascicularis (Kuala Lumpur, Malaysia)	MF1	9	22	449.1
	MF2	6	12	252.8
	MF3	6	18	293.0
	MF4	14	19	230.4
Macaca radiata (Thenmala, India)	MR1	24	22	553.2
	MR2	10	18	319.8

We used the proportion of AFR in the diet as a proxy for access to such food resources, on the premise that individuals prefer AFR food over natural food. This is indicated by a significant lower intake of natural food in provisioned animals (Maibeche et al., 2015; Sengupta and Radhakrishna, 2018; Sha and Hanya, 2013). AFR were defined as all food items that humans brought into or cultivated in the study area (Kaburu et al. 2019a; Kaburu et al. 2019b). We recorded the general activity (including feeding on either natural or AFR) through instantaneous sampling every two minutes within ten-minute focal observations. Individuals with less than 30 data points (i.e., 2 min instantaneous records) were excluded from further analyses. In addition, only records where the observer unambiguously identified the food item were included. These observations accounted for more than 80% of all feeding observations. Interobserver reliability between the observers were all above 0.85 as assessed by Cohen's kappa (Martin and Bateson, 1993). To calculate dominance ranks, we recorded all dyadic displacements (approach/leave interactions), submissions, and aggressive interactions between individuals with a clear winner/loser outcome during focal sampling and *ad libitum* sampling. For both males and females, a separate hierarchy was calculated using the package *Perc* in R (Fujii et al., 2016). A

linearity and steepness test in in R (R Development Core Team, 2009) using the package "Steepness" (Leiva and de Vries, 2011) revealed that all dominance hierarchies were significantly steep and linear. We further standardized ordinal ranks to account for group size and created a rank index ranging between zero and one, indicating the bottom and top ranking macaque respectively (see Kaburu et al., 2019b).

We used a Generalized Linear Mixed Model (GLMM) to determine individual differences in the proportion of anthropogenic food intake. The outcome variable was the total number of instantaneous records in which the individual was observed feeding on AFR. Sex and rank were the predictor variables. Species was included as a control variable due to potential inter-species differences in macaques' propensities to interact with humans. In addition, group was included in the model as a random effect. The total number of instantaneous records with a clearly defined food object was used as an offset in the model. We analyzed the data in R (R Development Core Team, 2009) using the 'lme4' package (Bates and Maechler, 2010). We used a negative binomial model, as the initial Poisson GLMM indicated an over-dispersion of the data. The predictors did not reveal auto-correlation during model diagnostics (using variance inflation factors).

Results:

We recorded 25,371 instantaneous records from 319 individuals across the nine study groups. The null model was significantly different from the full model (chi^2 = 42.70, df= 7, P < 0.001) and the predictors explained most of the observed variance in the outcome variable (conditional effect size R^2 = 0.81).

Both sex and rank significantly predicted the proportion of anthropogenic food intake. Specifically, males consumed anthropogenic food significantly more often than females did (Table 2, Figure 1). Similarly, higher-ranking individuals were more often observed feeding on anthropogenic food than were lower-ranking individuals (Table 2). Long-tailed macaques on average consumed more anthropogenic food than the two other species.

Table 2: Results from the GLMM investigating the predictors for the proportion of anthropogenic food intake.

	Estimate	Std. Error	z-value	Pr(>|z|)
(Intercept)	-1.13	0.20	-5.59	**<0.001**
Species (Long-tailed macaques)	0.77	0.24	3.15	**0.002**
Species (Rhesus macaques)	-0.18	0.25	-0.73	0.467
Sex (Males)	0.16	0.03	5.08	**<0.001**
Rank	0.11	0.05	2.29	**0.022**

Significant *P* values are indicated in bold.

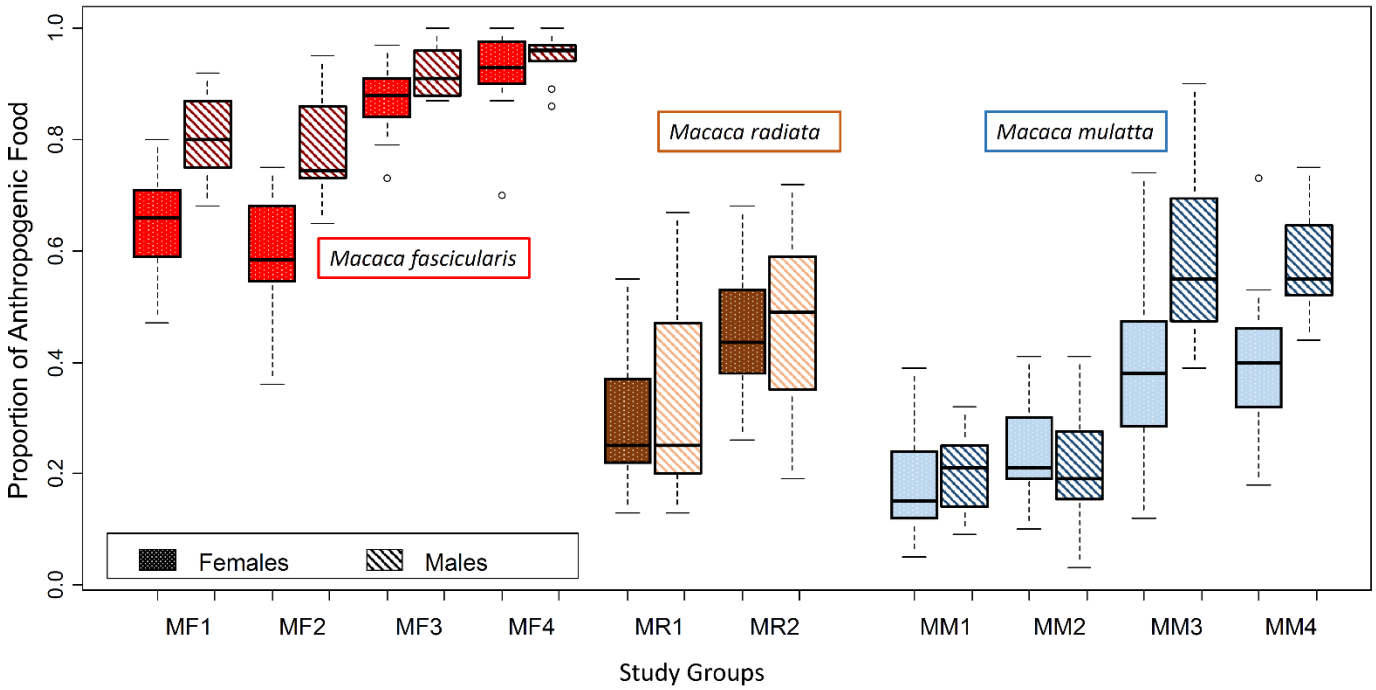

Figure 1: Proportion of anthropogenic food intake recorded during 2-min instantaneous records. Solid horizontal lines represent the medians; box height corresponds to the interquartile range; whiskers indicate the maximum and minimum values; dots represent outliers. MF = *Macaca fascicularis*, MR = *Macaca radiata*, MM = *Macaca mulatta*.

Discussion:

Our study shows that the benefits of living in an anthropogenic environment are unequally distributed across group members in urban dwelling macaques. Specifically, males and high-ranking individuals consume more AFR than other individuals do, indicating greater access to such food resources for these classes of individuals.

We suggest that the main determinant of the observed pattern is the higher monopolization potential of some individuals. In all macaques, males generally outrank females due to a moderate to strong sexual dimorphism in body mass and a strong to extreme dimorphism in canine size (Plavcan, 2001). Within their own hierarchy, both males and females with a higher rank were able to access AFR more frequently, most likely due to their ability to

224 successfully displace lower-ranking individuals from preferred food sources. Our observation is
225 in line with a previous experimental study showing that dominant individuals do monopolize
226 AFR (Kaplan et al., 2011). Similarly, our results support previous studies on rank differences in
227 access to AFR for female Japanese macaques under professionally provisioned conditions (e.g.,
228 Soumah and Yokota 1991; Mori 1995). However, they are contradictory to a study on bonnet
229 macaques living in a comparable environment with opportunistic provisioning from visitors
230 (Ram et al. 2003) which did not find a rank difference in the frequency of feeding on AFR
231 compared to natural food. These differences in results are likely due to the low sample size in
232 the Ram et al. (2003)'s study compared to our study or differences in the spread or amount of
233 the provisioned AFR.

234 Rank and sex differences in access to food are not restricted to AFR but are expected to
235 apply to natural food resources as well. High-ranking individuals in general, are expected to
236 have priority of access to preferred food resources in both urban and forested environments
237 (e.g., Fedigan 1983). In females, high-ranking individuals are known to grow faster, mature
238 earlier and show shorter interbirth intervals than low-ranking individuals, and all these factors
239 increase their fitness (reviewed in Harcourt 1987). In males, access to food resources
240 determines body mass, which is often positively associated with rank in the wild (e.g., Dittus,
241 1977; Dixson et al., 1993; Fragaszy et al., 2016; Marty et al., 2017). Access to preferred, high
242 caloric food resources due to high rank can therefore be expected to help preserve a certain
243 body mass, enabling males to maintain a high rank.

244 Even though the evolutionary implications of access to natural and AFR are similar, the
245 potential impact on an individual's health and fitness differs due to certain unique

characteristics of AFR. Anthropogenic food is generally high in calories (McLennan and Ganzhorn, 2017; Riley et al., 2013), and is likely to be more abundant, clumped, and more predictable in their spatial and temporal distribution than natural food (Becker and Hall, 2014; Koganezawa and Imaki, 1999; Saj et al., 1999; Strum, 1994; Warren et al., 2011). As a result, it is likely that the monopolization potential of AFR exceeds that of natural food resources. This may specifically be the case in situations where humans provide spatially and temporally predictable AFR (professional provisioning/garbage sites). Yet, our results indicate that the monopolization potential is still high even if the predictability is lowered through opportunistic provisioning. In general, access to AFR may further increase within-group competition over food resources (e.g. Southwick et al., 1976), increase selective advantages for high-ranking individuals regarding their reproductive success, and may positively affect high-ranking male tenure. However, whether, or to what degree, low-ranking individuals with restricted access to AFR benefit from an anthropogenic environment compared to individuals living in forested groups, remains to be investigated.

Similar to the benefits of access to AFR, the costs associated with such resources may also not be equally distributed across individuals but rather accumulate in individuals with increased access to such food resources Indeed, Sugiyama et al. (2014) found more congenital malformations related to access to AFR in male Japanese macaques compared to females. In a similar case in olive baboons (*Papio anubis*), diseases such as tuberculosis were found to spread primarily in males that were feeding on AFR, ultimately leading to the death of all males eating such food. Females were left unaffected as they were not feeding on these infected sources of AFR (Sapolsky and Share, 2004). Species and sex-specific differences in reproductive patterns

may also bias the trade-off between costs and benefits of access to AFR. In species where males have a very short reproductive period (high reproductive skew and short tenure, e.g., Crested macaques, *Macaca nigra*; (Marty et al., 2017)), short term benefits associated with AFR (e.g., increased body mass) might outweigh the long-term costs as these costs are likely to manifest later in life after the benefits of increased fitness have been received. Alternatively, for males in species with a relatively longer reproductive period and more generally for females, these long-term costs may affect their fitness more substantially. Yet, a generally shorter interbirth interval, lower infant mortality and higher population densities in many provisioned populations indicate that the benefits still outweigh the cost of access to AFR (Altmann and Muruthi, 1988; Jaman and Huffman, 2013; Kurita et al., 2008; Sugiyama and Ohsawa, 1982; Warren et al., 2011).

While patterns of access to AFR were consistent for males and high-ranking individuals within and across groups, we observed marked differences in the total proportion of AFR in the diet between groups. These differences, however, can be explained by differences in exposure to sources of AFR (visitors and locals). Among the long-tailed macaque populations we studied, for example, two groups lived in an area with more than 4000 visitors per day whereas the other two groups lived in a recreational park with around 150 visitors a day (Marty et al. 2019). Thus, the population with a higher exposure to visitors have higher proportions of AFR in their diet. This result shows that access to AFR is not dependent on the quantity of the AFR provided but rather shows the same pattern across different levels of opportunistic provisioning.

Our results highlight the importance of investigating inter-individual differences in cost-benefit assessments of living in an urban environment, in addition to group level differences.

Selection pressures specifically might be elevated in urban environments as a consequence of increased competition over AFR. However, more comparative and individual-based data are needed to reveal whether and how these differences in selection pressures differentially impact the long-term behavior, health and fitness of individuals living in urban and forested groups.

Acknowledgments

We are thankful to the Economic Planning Unit Malaysia, the Forestry Department of Peninsular Malaysia, the Department of Wildlife and National Parks Peninsular Malaysia, Tourism Selangor, the Kerala Forest and Wildlife Department, and the Himachal Pradesh Forest Department for giving permission to conduct our research in Malaysia and India. We thank our research assistants Camille Luccisano, Eduardo Saczek, Silvia La Gala, Nur Atiqua Tahir, Shelby Samartino, Rachael Hume, Taniya Gill, Kawaljit Kaur, Bidisha Chakraborty, Benjamin Sipes, Nalina Aiempichitkijkarn Pooja Dongre, Mohammed Ismail, Megha Majoe, Rajarshi Saha, Alvaro Sobrino, and Menno Van Berkel for their help in collecting data. This work was supported by the U.S. National Science Foundation (grant no. 1518555).

References:

Altmann, J., Muruthi, P., 1988. Differences in daily life between semiprovisioned and wild-feeding baboons. Am. J. Primatol. 15, 213–221. https://doi.org/10.1002/ajp.1350150304

Bates, D., Maechler, M., 2010. Linear mixed-effects models using S4 classes.

Becker, D.J., Hall, R.J., 2014. Too much of a good thing: resource provisioning alters infectious disease dynamics in wildlife. Biol. Lett. 10, 20140309–20140309. https://doi.org/10.1098/rsbl.2014.0309

Berman, C.M., Li, J., Ogawa, H., Ionica, C., Yin, H., 2007. Primate tourism, range restriction, and infant risk among Macaca thibetana at Mt. Huangshan, China. Int. J. Primatol. 28, 1123–1141. https://doi.org/10.1007/s10764-007-9199-4

Berman, C.M., Li, J.H., 2002. Impact of translocation, provisioning and range restriction on a

group of Macaca thibetana. Int. J. Primatol. 23, 383–397. https://doi.org/10.1023/A:1013891730061
Dittus, W.P.J., 1977. The social regulation of population density and age-sex distribution in the toque monkey. Behaviour 281–322.
Dixson, A.F., Bossi, T., Wickings, E.J., 1993. Male dominance and genetically determined reproductive success in the mandrill (Mandrillus sphinx). Primates 34, 525–532. https://doi.org/10.1007/BF02382663
El Alami, A., Van Lavieren, E., Rachida, A., Chait, A., 2012. Differences in Activity Budgets and Diet Between Semiprovisioned and Wild-Feeding Groups of the Endangered Barbary Macaque (Macaca sylvanus) in the Central High Atlas Mountains, Morocco. Am. J. Primatol. 74, 210–216. https://doi.org/10.1002/ajp.21989
Fa, J.E., 1985. Provisioning of Barbary macaques on the Rock of Gibraltar, in: Box, H.O. (Ed.), Primate Responses to Environmental Change. SPRINGER-SCIENCE+BUSINESS MEDIA, B.V., Bristol, pp. 137–153.
Fedigan, L.M., 1983. Dominance and reproductive success in primates. Am. J. Phys. Anthropol. 26, 91–129. https://doi.org/10.1002/ajpa.1330260506
Fragaszy, D.M., Izar, P., Liu, Q., Eshchar, Y., Young, L.A., Visalberghi, E., 2016. Body mass in wild bearded capuchins, (Sapajus libidinosus): Ontogeny and sexual dimorphism. Am. J. Primatol. 78, 473–484. https://doi.org/10.1002/ajp.22509
Fujii, K., Jin, J., Shev, A., Beisner, B., McCowan, B., Fushing, H., 2016. Perc: Using Percolation and Conductance to Find Information Flow Certainty in a Direct Network. R Packag. version 0.1.2. http://CRA.
Harcourt, A.H., 1987. Dominance and Fertility among Female Primates. J. Zool. 213, 471–487.
Hernandez-Pacheco, R., Delgado, D.L., Rawlins, R.G., Kessler, M.J., Ruiz-Lambides, A. V., Maldonado, E., Sabat, A.M., 2016. Managing the Cayo Santiago rhesus macaque population: The role of density. Am. J. Primatol. 78, 167–181. https://doi.org/10.1002/ajp.22375
Ilham, K., Rizaldi, Nurdin, J., Tsuji, Y., 2018. Effect of Provisioning on the Temporal Variation in the Activity Budget of Urban Long-Tailed Macaques (Macaca fascicularis) in West Sumatra , Indonesia. Folia Primatol. 25163, 347–356. https://doi.org/10.1159/000491790
Jaman, M.F., Huffman, M.A., 2013. The effect of urban and rural habitats and resource type on activity budgets of commensal rhesus macaques (Macaca mulatta) in Bangladesh. Primates 54, 49–59. https://doi.org/10.1007/s10329-012-0330-6
Kaburu, Stefano S.K., Beisner, B., Balasubramaniam, K.N., Marty, P.R., Bliss-Moreau, E., Mohan, L., Rattan, S.K., Arlet, M.E., Atwill, E.R., McCowan, B., 2019. Interactions with humans impose time constraints on urban-dwelling rhesus macaques (Macaca mulatta). Behaviour 1–28. https://doi.org/10.1163/1568539X-00003565
Kaburu, Stefano S. K., Marty, P.R., Beisner, B., Balasubramaniam, K.N., Bliss-Moreau, E., Kaur, K., Mohan, L., McCowan, B., 2019. Rates of human-macaque interactions affect grooming behavior among urban-dwelling rhesus macaques (Macaca mulatta). Am. J. Phys. Anthropol. 168, 92–103. https://doi.org/10.1002/ajpa.23722
Kaplan, B.S., O'Riain, M.J., van Eeden, R., King, A.J., 2011. A Low-Cost Manipulation of Food Resources Reduces Spatial Overlap Between Baboons (Papio ursinus) and Humans in Conflict. Int. J. Primatol. 32, 1397–1412. https://doi.org/10.1007/s10764-011-9541-8

363 Koganezawa, M., Imaki, H., 1999. The Effects of Food Sources on Japanese Monkey Home
364 Range Size and Location, and Population Dynamics. Primates 40, 177–185.
365 https://doi.org/10.1007/BF02557709
366 Kurita, H., 2007. Comparison of artificial food intake between high- and low-ranking females
367 among provisioned, free-ranging Japanese macaques (Macaca fuscata) at Takasakiyama -
368 Preliminary report. Primate Res. 23, 25–32. https://doi.org/10.2354/psj.23.25
369 Kurita, H., Sugiyama, Y., Ohsawa, H., Hamada, Y., Watanabe, T., 2008. Changes in demographic
370 parameters of Macaca fuscata at Takasakiyama in relation to decrease of provisioned
371 foods. Int. J. Primatol. 29, 1189–1202. https://doi.org/10.1007/s10764-008-9296-z
372 Leiva, D., de Vries, H., 2011. Testing Steepness of Dominance Hierarchies.
373 Maibeche, Y., Moali, A., Yahi, N., Menard, N., 2015. Is diet flexibility an adaptive life trait for
374 relictual and peri-urban populations of the endangered primate Macaca sylvanus? PLoS
375 One 10, 1–22. https://doi.org/10.1371/journal.pone.0118596
376 Malaivijitnond, S., Hamada, Y., 2008. Current Situation and Status of Long-tailed Macaques
377 (Macaca fascicularis) in Thailand. Trop. Nat. Hist. 8, 185–204.
378 Marechal, L., Semple, S., Majolo, B., Qarro, M., Heistermann, M., MacLarnon, A., 2011. Impacts
379 of tourism on anxiety and physiological stress levels in wild male Barbary macaques. Biol.
380 Conserv. 144, 2188–2193. https://doi.org/10.1016/j.biocon.2011.05.010
381 Martin, P., Bateson, P., 1993. Measuring behaviour. Cambridge university press, Cambridge.
382 Marty, P.R., Beisner, B., Kaburu, S.S.K., Balasubramaniam, K., Bliss-Moreau, E., Ruppert, N., Sah,
383 S.A.M., Ismail, A., Arlet, M.E., Atwill, E.R., McCowan, B., 2019. Time constraints imposed by
384 anthropogenic environments alter social behaviour in long-tailed macaques. Anim. Behav.
385 150, 157–165. https://doi.org/10.1016/j.anbehav.2019.02.010
386 Marty, P.R., Hodges, K., Agil, M., Engelhardt, A., 2017. Alpha male replacements and delayed
387 dispersal in crested macaques (*Macaca nigra*). Am. J. Primatol. 79, e22448.
388 https://doi.org/10.1002/ajp.22448
389 McCarthy, M.S., Matheson, M.D., Lester, J.D., Sheeran, L.K., Li, J., Wagner, R.S., 2009.
390 Sequences of Tibetan Macaque (Macaca thibetana) and Tourist Behaviors at Mt.
391 Huangshan, China. Primate Conserv. 24, 145–151. https://doi.org/10.1896/052.024.0113
392 McKinney, T., 2011. The effects of provisioning and crop-raiding on the diet and foraging
393 activities of human-commensal white-faced Capuchins (Cebus capucinus). Am. J. Primatol.
394 73, 439–448. https://doi.org/10.1002/ajp.20919
395 McLennan, M.R., Ganzhorn, J.U., 2017. Nutritional Characteristics of Wild and Cultivated Foods
396 for Chimpanzees (Pan troglodytes) in Agricultural Landscapes. Int. J. Primatol. 38, 122–150.
397 https://doi.org/10.1007/s10764-016-9940-y
398 Mori, A., 1995. Rank and age related feeding strategy observed through field experiments in the
399 Koshima group of Japanese macaques. Primates 36, 11–26.
400 https://doi.org/10.1007/BF02381912
401 Oro, D., Genovart, M., Tavecchia, G., Fowler, M.S., Martínez-Abraín, A., 2013. Ecological and
402 evolutionary implications of food subsidies from humans. Ecol. Lett. 16, 1501–1514.
403 https://doi.org/10.1111/ele.12187
404 Plavcan, J., 2001. Sexual dimorphism in primate evolution. Am. J. Phys. Anthropol. 53, 25–53.
405 https://doi.org/10.1002/ajpa.10011
406 R Development Core Team, 2009. R: A language and environment for statistical computing.

Ram, S., Venkatachalam, S., Sinha, A., 2003. Changing social strategies of wild female bonnet macaques during natural foraging and on provisioning. Curr. Sci. 84, 780–790. https://doi.org/https://www.jstor.org/stable/24107582

Riley, E.P., Tolbert, B., Farida, W.R., 2013. Nutritional content explains the attractiveness of cacao to crop raiding Tonkean macaques. Curr. Zool. 59, 160–169. https://doi.org/10.1093/czoolo/59.2.160

Saj, T., Sicotte, P., Paterson, J.D., 1999. Influence of Human Food Consumption on the Time Budget of Vervets. Int. J. Primatol. 20, 974–977. https://doi.org/10.1023/A:1020886820759

Sapolsky, R.M., Share, L.J., 2004. A pacific culture among wild baboons: its emergence and transmission. PLoS Biol. 2, E106. https://doi.org/10.1371/journal.pbio.0020106

Sengupta, A., Radhakrishna, S., 2018. The Hand That Feeds the Monkey: Mutual Influence of Humans and Rhesus Macaques (Macaca mulatta) in the Context of Provisioning. Int. J. Primatol. 39, 817–830. https://doi.org/10.1007/s10764-018-0014-1

Sha, J.C.M., Hanya, G., 2013. Diet, Activity, Habitat Use, and Ranging of Two Neighboring Groups of Food-Enhanced Long-Tailed Macaques (Macaca fascicularis). Am. J. Primatol. 75, 581–592. https://doi.org/10.1002/ajp.22137

Soumah, A.G., Yokota, N., 1991. Female Rank and Feeding Strategies in a Free-Ranging Provisioned Troop of Japanese Macaques. Folia Primatol. 57, 191–200. https://doi.org/https://doi.org/10.1159/000156586

Southwick, C.H., Siddioi, M.F., Farooqui, M.Y., Pal, B.C., 1976. Effects of artificial feeding on aggressive behaviour of rhesus monkeys in India. Anim. Behav. 24, 11–15. https://doi.org/10.1016/S0003-3472(76)80093-0

Strum, S.C., 1994. Prospects for management of primate pests. Rev. d'Ecologie La Terre La Vie 49, 295–306.

Sugiyama, Y., Kurita, H., Matsui, T., Kimoto, S., Egawa, J., 2014. Congenital malformations in Japanese macaques (Macaca fuscata) at Takasakiyama. Primates 55, 303–311. https://doi.org/10.1007/s10329-014-0405-7

Sugiyama, Y., Ohsawa, H., 1982. Population Dynamics of Japanese Monkeys with Special Reference to the Effect of Artifical Feeding. Folia Primatol. 39, 238–263.

Warren, Y., Higham, J.P., Maclarnon, A.M., Ross, C., 2011. Crop-raiding and Commensalism in Olive Baboons: The Costs and Benefits of Living with Humans, in: Sommer, V., Ross, C. (Eds.), Primates of Gashaka. Springer, Chicago, pp. 307–332.

Yeager, C.P., 1996. Feeding ecology of the long-tailed macaque (Macaca fascicularis) in Kalimantan Tengah, Indonesia. Int. J. Primatol. 17, 51–62. https://doi.org/10.1007/BF02696158